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ABSTRACT

Territory quality is often critical for reproductive success, survival and, ultimately, fitness. Holding a good qual-ity territory can make a male more attractive to females but can also have several other advantages. It can decrease the effects of environmental stressors, for example, by reducing the need for behavioural thermoregula-tion or decreasing the risk of predation. We found that, in the fiddler crab *Austruca mjoebergi*, male territories differed in the shaded mangrove and unshaded open areas of the habitat. The lower temperatures and wetter sediments of the mangrove areas resulted in lower desiccation rates allowing males to spend longer periods of time on the surface than they did in the sun-exposed open areas. Males lived at higher densities in the mangrove areas, and preferentially selected shaded territories when given a choice. Male fights to attain/retain territories in the mangrove areas were longer than those in the open areas. Because females do not preferentially mate with males with territories in shaded mangrove habitats, the advantages to males in maintaining these territories is likely a reduction in thermal and/or desiccation stress.

1. Introduction

In sexually selected species, males often maintain and defend territories. In heterogeneous landscapes, habitat quality differs across the landscape and habitat preference during territory establishment can be a critical factor driving reproductive success, survival, and ultimately fitness. Territory quality is often directly associated with mating success (Balmford et al., 1992; Weatherhead and Robertson, 1977; Wells, 1977) because females prefer males occupying territories with certain characteristics (Johnsson et al., 2000). In other cases, territory quality may confer advantages not directly associated with mating, but rather associated with variation in resource availability (Rubenstein, 1984), or an individual's ability to avoid heat stress, desiccation (Mathis, 1990) and predation (Johnsson et al., 2004). Therefore in heterogeneous landscapes, selecting a high-quality territory can reduce costs, such as those associated with behavioural thermoregulation.

Fiddler crabs offer a good model system to explore the importance of territory quality and the factors driving territory preferences. Fiddler crabs live in heterogeneous intertidal habitats that are often physiologically challenging (e.g., Allen and Levinton, 2014; Darnell et al., 2015; Munguia et al., 2017). *Austruca mjoebergi* males display to females on the surface and defend their burrow opening against other males. They are exposed to severe heat and desiccation stress while on the surface and must retreat into their burrow to cool off and rehydrate at regular intervals (Munguia et al., 2017). Greater time spent on the surface results in greater time available to feed, defend a territory, and attract females; therefore, retreating into the burrow can be costly. The habitat of *A. mjoebergi* is characterized by a heterogeneous matrix of microhabitats, with open un-shaded areas of mudflat interspersed with areas shaded by mangroves (e.g., Fig. 1). High densities of males are observed under the mangrove canopy, suggesting that this habitat may represent a preferred territory location (Munguia et al., 2017), although high density alone does not necessarily indicate habitat preference, as density differences between microhabitats could be due to factors other than habitat selection (Pulliam, 1988; Horne, 1983). Chou et al. (*in review*) found that the likelihood of mating in *A. mjoebergi* did not differ between the mangrove and open habitats during the mating season, and when given a choice between a male in shade and a male exposed to sun, females showed no preference (Chou et al. *in review*). If male *A. mjoe-*

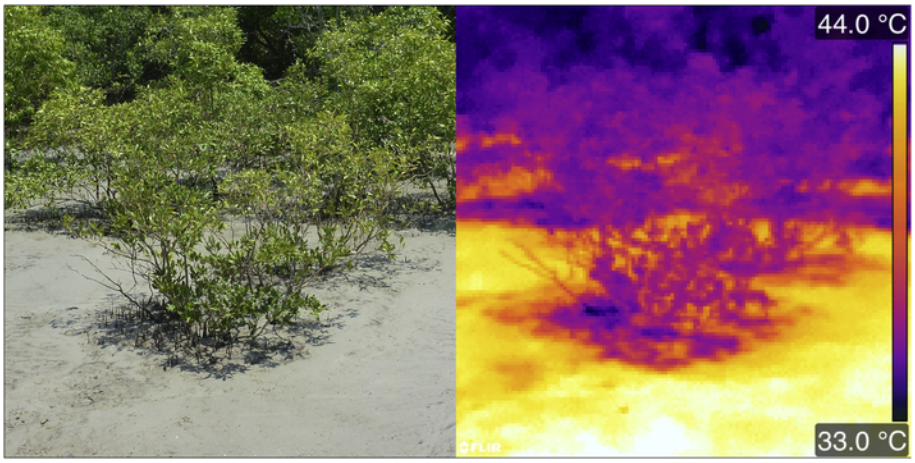

Fig. 1. Image of a single mangrove bush at the study site in visible light (left) and infrared (right), showing the thermal heterogeneity of the *Austruca mjoebergi* habitat. Images were taken at ~13:00.

bergi do show a preference for the mangrove habitat, that preference is thus likely driven by factors other than mating success.

Here, we explore whether mangrove fiddler crabs preferentially establish territories in shaded habitats on the mudflat over open un-shaded ones, the strength of any preferences that exist and the possible advantages that accrue to males that are selective in their territory choice. To do so we determined (i) the density and size distributions of male crabs in two distinct habitats: a mangrove-shaded habitat and an open, un-shaded habitat, (ii) whether males show a preference for shaded or unshaded habitats when choosing a territory location, (iii) the duration and escalation of territorial combat in mangrove-shaded and open, unshaded habitats (since territory defence is often associated with habitat quality and preference (Johnsson et al., 2000) we used this as a measure of differences in the "value" of territories to males), (iv) differences in environmental conditions between the two habitats, specifically desiccation rates and water and food availability, in the sediment, and (v) differences in time spent on the surface vs. in the burrow in each of the two habitats.

2. Materials and methods

2.1. Study species and site

Austruca (=Uca) mjoebergi is a small (<15 mm carapace width, <1.2 g wet mass) fiddler crab from north Australia. They live in dense, mixed-sex populations on intertidal mudflats (Reaney and Backwell, 2007). Males maintain and defend territories (~10 cm diameter) centred on a burrow. The surrounding surface is used for feeding and courting while the burrow serves as a mating site (Reaney and Backwell, 2007); a refuge from predation (Reaney, 2007), heat, and desiccation (Munguia et al., 2017); and a source of water (Reaney and Backwell, 2007). Males that have lost their territories initiate fights with residents attempting to win the territory. Fights also occur between neighbouring residents over the use of feeding areas near the territorial boundaries; these seldom result in an eviction of a crab from its burrow (Booksmythe et al., 2010). During the mating period (six days of neap tides each 14-day semilunar cycle), sexually receptive females wander through the population searching for a mate. Males perform species-specific waving display on the surface near their burrows to attract searching females. Females visit several males ($\bar{x} = 3$) before choosing a mate (Clark and Backwell, 2015). Mating occurs in the male's burrow, and the male then guards the female until oviposition (1–2 d after mating). The female remains in the burrow for the ~20 d incubation period until she re-emerges to release larvae (Reaney and Backwell, 2007) but the male emerges after oviposition to resume feeding, courting and mating. Female mate choice is based on multiple male traits (Holman et al., 2014; Mowles et al., 2017; Vega-Trejo and Backwell, 2017) as well as on the quality of the male's burrow (Reaney and Backwell, 2007). Females must select a burrow that prevents desiccation and tidal inundation, and that will remain structurally stable over the incubation period.

This study was conducted in November 2016 at East Point Reserve, Darwin, Northern Territory, Australia (12°24.53′S, 130°49.85′E). The study site covers an area of approximately 50 × 200 m and is characterized by a heterogeneous matrix of microhabitats, with open un-shaded areas of mud interspersed with areas shaded by mangroves. The site is inundated by spring tides for ±8 days each lunar cycle. Crabs are surface-active during the diurnal low spring tides; this is the non-mating period and it is when crabs feed, fight and maintain their burrows. During the ±6 day neap tide period, the site is never inundated and the crabs remain surface active for most of the day (Reaney and Backwell, 2007). This is the mating period when females wander and males court. This study was conducted during the non-mating period to understand habitat constraints independent of the mating cycle.

2.2. Density and size distributions of male crabs in a mangrove-shaded habitat and an open, un-shaded habitat

To assess differences in the density of surface-active males in the two habitats, we placed quadrats (35 cm × 35 cm) either under the mangrove canopy (mangrove habitat) or in the unvegetated areas that are exposed to direct sunlight (open habitat). We placed two quadrats in each habitat each day for three days (six independent quadrats per habitat). For each quadrat, we counted the number of males on the surface each hour for two hours in the morning (1000–1100, 1100–1200) and three hours in the afternoon (1200–1300, 1300–1400, and 1400–1500). Counts were taken from open and mangrove quadrats almost simultaneously. Data were analyzed using a linear mixed effects models with $\log_{10}$(abundance on the surface +1) as the response variable, date and plot ID (nested within date) as random effects, and treatment and time period as fixed effects.

We examined crab size in the two habitats by measuring burrow diameters (these are closely correlated with occupant size: $r = 0.70$ (Reaney and Backwell, 2007)). A 15.5 × 15.5 cm quadrat was randomly placed in each habitat and the entrance width of all burrows

within the quadrat were measured using calipers. A total of 51 burrows were measured in each habitat. Burrows <6-mm in diameter ($n = 18$ in shade, $n = 7$ in sun) were excluded from analyses as these typically represent juvenile crabs and are difficult to measure accurately. Burrow diameters were log10-transformed prior to analyses, and compared between the two habitats using a *t*-test.

2.3. Male preference for burrows in shaded habitat and un-shaded habitats

In an unshaded, open area of the study site, we placed temporary circular enclosures constructed of 9-cm high opaque plastic collars that each enclosed a 53-cm diameter circle of sediment. We shaded half of each enclosure by erecting a frame with shade cloth above half of each enclosure; the other half of each enclosure was exposed to full sun. We created an equal number of uniformly spaced artificial burrows in each half by pushing a 6 mm diameter wooden dowel rod into the sediment at a 45° angle, to a depth of 45 mm. One of the enclosures had four artificial burrows in each half (low density treatment) and the other had eight burrows in each half (high density treatment). We placed four males (low density enclosure) or eight males (high density enclosure) on the central line delimiting the shaded and unshaded halves of the enclosure and left them undisturbed for three hours, free to move throughout the enclosure and select an artificial burrow in the shaded or unshaded parts of the enclosure. Because of the small size of the artificial burrows, crabs had to enlarge the burrows before they could use them. After three hours, we removed the shade cloth and noted the number of occupied (modified) burrows in each half of the enclosure. We used three replicates (three high and three low density enclosures) each day for three days resulting in a sample size of nine independent enclosures for each density. All experiments were conducted between 10:00 and 14:30.

We calculated the relative burrow density for each half of each of the 18 enclosures as the number of occupied burrows within the half of the enclosure divided by the total number of occupied burrows throughout the entire enclosure. These proportions were logit-transformed after adding a value of 0.143 (the minimum non-zero proportion observed; Warton and Hui, 2011) to all proportions. Data were analyzed using a linear mixed-effects model with logit(proportion of active burrows +0.143) as the response variable and date and enclosure ID (nested within date) as random effects. Habitat (shaded or unshaded) and density were included as fixed effects.

2.4. Duration and escalation of territorial combat in mangrove-shaded and open, unshaded habitats

We documented male fights in both habitats by releasing a focal male within a group of surface-active males and watching him until he initiated a fight with a resident. We recorded the fight duration from the time of first to last contact (either because the focal male successfully usurped the burrow and the original male left, or because the focal male retreated from the fight). We also recorded fight escalation as low or high: low escalation fights are those where males push the front surfaces of their large claws against each other; these fights may or may not escalate to grapples (high escalation flights) where males interlock claws. We documented 20 fights in each of the two habitats. We used a Chi-square test to examine the proportion of fights that escalated to grappling in each of the two habitats. Fight durations were analyzed using a two-way analysis of variance (ANOVA) with transformed ($\log_{10} + 1$ transformation) fight durations as the response variable, testing for effects of habitat, fight type, and a habitat x fight-type interaction.

2.5. Desiccation rates and food/water availability in shaded and unshaded habitats

We determined the desiccation rates of males under shaded and sun-exposed conditions. We collected males and immediately placed them in plastic cups containing ±3 cm of water (ambient temperature) from the collection site. Crabs were left in the cups for at least 20 min to ensure full hydration. Crabs were then blotted dry to remove excess surface water and weighed to the nearest 0.01 g. They were then placed in individual plastic containers (17 cm long × 12 cm wide × 8 cm high) with a mesh bottom and containing a thin layer of sediment. The containers were placed on the sediment, either under mangroves or in the open unshaded habitat. After 35–41 min, crabs were removed from the containers and re-weighed. Desiccation rates were standardized as percent body mass lost per minute. Ten crabs were confined in each habitat simultaneously on each of two days ($n = 20$ males per treatment). Data were analyzed using a linear mixed-effect model, with percent body mass lost per minute as the response variable, initial mass and habitat as fixed effects, and day as a random effect.

We determined the availability of food and sediment moisture content in both habitats. We collected sediment samples (± 5 g) by scraping up the top 2–3 mm of sediment. We weighed each sample and then dried them for 10 h at 60 °C to remove water, after which time they were re-weighed to determine dry mass. Sediment water content (g water per g sediment) was calculated as wet weight minus dry weight divided by wet weight. Samples were then placed in a 500 °C oven for 5 h to remove organic content, and then weighed to determine ash-free dry weight (AFDW). Sediment organic content (g organics per g sediment) was calculated as dry weight minus AFDW divided by dry weight. A total of 35 samples were collected, 18 from open habitat and 17 from mangrove habitat. Data were analyzed using *t*-tests (assuming unequal variances), with sediment water content and sediment organic content as response variables.

2.6. Duration of surface activity and burrow retreats in open and mangrove habitats

We assessed the amount of time that males spent on the surface between successive visits to their burrows and the amount of time spent in the burrow before emerging, in both habitats. We placed 35 cm × 35 cm quadrats randomly in each habitat and video-recorded the surface activity (from directly above the quadrat using a Sony Handicam DCR-SR45E) for ~1 h during the middle of the day (12:00–14:00) over two consecutive days. From the videos, we selected all males that were clearly visible (27 males in 9 quadrats in the open habitat; 19 males in 6 quadrats in the mangrove habitat; $\overline{x} = 3$ males per quadrat, range = 1–6). For each male, we noted the duration of surface activity between two successive visits to the burrow. We also noted the time spent inside the burrow before re-emerging. Time on the surface and time in the burrow were log10-transformed and analyzed using linear mixed effects models with day as a random effect and habitat as a fixed effect.

2.7. Ethical note

This research was conducted under an Australian National University Animal Ethics permit (A2015/54) and under a research permit from the Darwin City Council (permit no. 3648724). The protocols used are reliable, commonly used methods that are designed to minimize mortality and stress. We limited the handling and the amount of time each crab was used as much as possible. No crab was

injured during the research, and they all continued their regular activities after release.

3. Results

3.1. Density and size distributions of male crabs in a mangrove-shaded habitat and an open, un-shaded habitat

The number of males on the surface differed between the two habitats, with greater male surface activity in the mangrove habitat than the open habitat ($F_{1,99.32} = 78.378$, $P < .0001$). On average, 3.8 ± 0.2 (mean ± SE) male crabs were active in each quadrat in the mangrove habitat, while 1.4 ± 0.2 male crabs were active in each quadrat in the open habitat. There was no significant effect of time period ($F_{1,93.99} = 1.830$, $P = .130$), and there was no significant time x treatment interaction ($F_{1,99.32} = 2.248$, $P = .069$).

Burrow entrance diameter did not differ between the two habitats ($t = 0.655$, DF = 65.011, $P = .515$). Excluding burrows <6 mm in diameter, burrow diameter averaged 9.51 ± 0.26 mm.

3.2. Male preference for burrows in shaded habitat and un-shaded habitats

Following the 3-h experiment, occupied burrow density in the shaded half of the enclosures averaged 14.6 ± 2.9 burrows m^{-2} in the low density treatment and the 24.2 ± 3.4 burrows m^{-2} in the high density treatment, while occupied burrow density in the unshaded half of the enclosures averaged 4.0 ± 1.6 burrows m^{-2} in the low density treatment and 9.6 ± 2.4 burrows m^{-2} in the high density treatment. A significantly greater proportion of occupied burrows were in the shaded half of the enclosure than the unshaded half ($F_{1,22} = 65.383$, $P < .0001$), and this trend did not differ between the two density treatments ($F_{1,22} = 1.7791$, $P = .196$; Fig. 2).

3.3. Duration and escalation of territorial combat in mangrove-shaded and open, unshaded habitats

The resident male was nearly always successful in defending his burrow with 92.5% ($n = 37$) of fights won by the resident and 7.5% (n = 3) won by the intruder. The proportion of fights escalating to a grapple did not differ between the two habitats ($\chi^2 = 0.405$, $P = .525$). Fight duration was longer in the mangrove than in the open habitat (18.8 ± 4.2 s vs 6.9 ± 1.5 s; $F_{1,1} = 5.222$, $P = .030$; Fig. 3). Additionally, fights that escalated to a grapple were longer than fights consisting solely of pushing (23.0 ± 4.1 s vs 4.9 ± 3.7 s; $F_{1,1} = 3.407$, $P < .0001$).

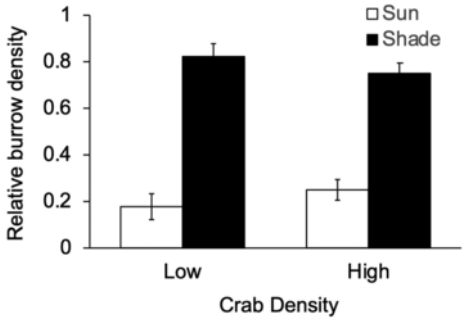

Fig. 2. Relative burrow density (proportion of total active burrows in the arena that were located in that half of the arena) for unshaded and shaded sides of experimental arenas, under low or high male density. Relative burrow density was significantly in the shaded half of the enclosure than the unshaded half ($F_{1,22} = 65.383$, $P < .0001$), and this trend did not differ between the two density treatments ($F_{1,22} = 1.7791$, $P = .196$).

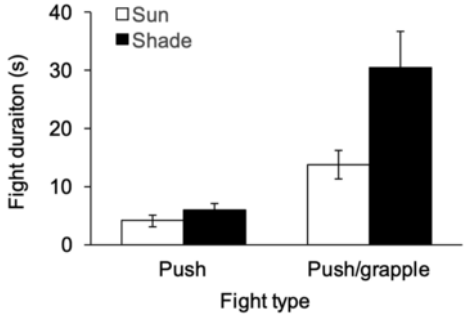

Fig. 3. Fight duration for fights consisting of only pushing or escalating to a grapple, when an intruder was introduced into a mangrove-shaded or open, unshaded area. Fight duration was longer in the mangrove than in the open habitat ($F_{1,1} = 5.222$, $P = .030$). Fights that escalated to a grapple were longer than fights consisting solely of pushing ($F_{1,1} = 3.407$, $P < .0001$). There was no significant habitat x fight type interaction ($F_{1,1} = 0.928$, $P = .342$).

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3.4. Desiccation rates and food/water availability in shaded and unshaded habitats

Crabs in the open habitat desiccated at a significantly faster rate than crabs within the mangroves ($F_{1,35.42} = 19.615$, $P < .0001$). Crabs in the open lost on average 0.125 ± 0.015% of their body mass per minute, while crabs in the mangroves lost on average 0.017 ± 0.017% of their body mass per minute. There was no significant effect of initial body mass on desiccation rates ($F_{1,25.93} = 0.2313$, $P = .635$) and no significant initial mass x habitat interaction ($F_{1,35} = 2.461$, $P = .126$).

Sediment water content differed significantly between the sun and shade ($t = -4.332$, DF = 32.618, $P < .0001$). Sediment in the shade contained 31.67 ± 3.61% water, while sediment in the sun contained 26.51 ± 3.43% water. Organic content did not differ between the two habitats ($t = 1.325$, DF = 30.022, $P = .1953$). Sediment in the shade contained 6.60 ± 2.21% organics, while sediment in the sun contained 7.84 ± 3.26% organics.

3.5. Duration of surface activity and burrow retreats in open and mangrove habitats

Time in the burrow did not differ between the two habitats ($F_{1,21.25} = 1.659$, $P = .212$; Fig. 4). On average, crabs spent 28.05 ± 3.93 s in the burrow before emerging. Time spent on the surface between retreats to the burrow differed significantly between the two habitats ($F_{1,21.91} = 8.477$, $P = .008$; Fig. 4), with crabs in the sun spending 301.69 ± 52.92 s on the surface before retreating to the burrow and crabs in the shade spending 1014.44 ± 243.32 s on the surface before retreating to the burrow.

4. Discussion

We examined habitat preferences in the fiddler crab *Austruca mjoebergi* during the non-mating phase of the lunar cycle, and several characteristics of the habitats that could contribute to these preferences. *Austruca mjoebergi* inhabits a hot tropical habitat, with high risk of thermal and desiccation stress, especially during the day when crabs are active on the sediment surface. Males cluster in shaded areas near mangrove trees, and show a clear preference for shaded territories. Our results suggest that the shade provides refuge from desiccation and heat stress as these areas have greater moisture (results presented here) and lower temperatures (Munguia et al., 2017) than

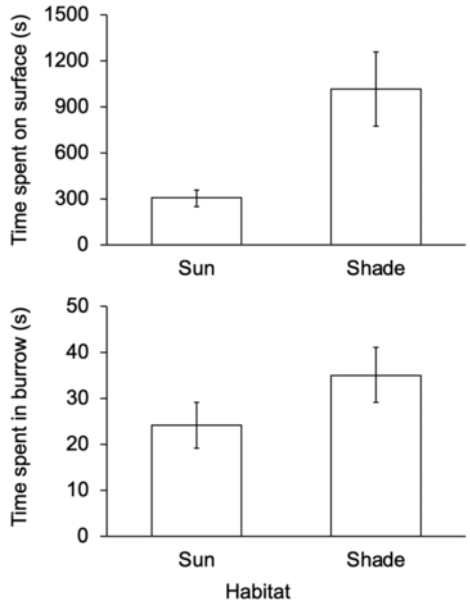

Fig. 4. Duration of surface activity and burrow retreats in open, unshaded or mangrove-shaded habitats. Time in the burrow did not differ between the two habitats ($F_{1,21.25} = 1.659$, $P = .212$). Time spent on the surface between retreats to the burrow differed significantly between the two habitats ($F_{1,21.91} = 8.477$, $P = .008$).

open spaces. Such refuge from heat might be sufficient to drive high crab densities in these shaded areas as shown in this study. Territory quality, in the case of *A. mjoebergi*, is driven by physiological needs.

Male fiddler crabs maintain burrow-centered territories for short periods of time averaging a 3-day residency per burrow (Backwell, unpublished data.). The male's burrow is a critical component of male mating success as it is a resource sought by females as the site of copulation, and egg incubation (Reaney and Backwell, 2007). However, given that fiddler crabs are operating very close to their upper thermal limit, burrows also offer refuge from the high temperatures typical of tropical mangrove forests (Munguia et al., 2017) during both the mating and the non-mating period.

In this study, when given a choice, male *A. mjoebergi* showed a strong preference for establishing burrows in shaded over un-shaded territories in experimental enclosures even at high male densities. In some cases this resulted in burrow densities of up to ~36 burrows m^{-2}. These results suggest that the benefit of being in the shade is great enough to mitigate the potential costs of having a small territory and being near many other males (e.g., greater competition for potential mates, increased frequency of antagonistic interactions). Given that female *A. mjoebergi* do not show a preference for males occupying shaded territories (Chou et al., *In review*), male territory preferences appear be driven by thermal stress and desiccation risk. Fiddler crabs experience substantially higher body temperatures in the open, unshaded habitat relative to the mangrove habitat, approaching their upper thermal limit during much of the day, while the shade of the mangrove canopy provides a refuge from thermal stress (Munguia et al., 2017). This study showed that desiccation rates are reduced under the mangrove canopy due to the greater water content of the sediment and reduced evaporation rates.

If burrows in shaded habitats are a more valuable resource and provide better refuge from thermal stress than burrows in open habitats, one would expect males to defend them more vigorously. We observed that male-male fights for territories were longer in the mangrove habitat than in the open unshaded habitat providing some support for this hypothesis. However, it is also possible that differences in fight duration reflect differences in thermal or desiccation stress between the two habitats; shorter fight durations in the open habitat could be driven by the physiologically stressful nature of combat, combined with the high temperatures experienced on the open, unshaded sediment surface (Munguia et al., 2017). Intruder males may be unable to continue fighting and give up sooner in open habitat than in the shaded mangrove habitat, where temperatures are lower.

One significant advantage of the reduced risk of thermal and desiccation stress in mangrove shaded habitats is that it allows males to remain on the surface for longer than males in open, unshaded areas. We found a greater number of males were active on the surface in mangrove habitats compared to open habitats and individual males in mangrove habitats remained on the surface for longer periods between burrow visits. This suggests that males in shaded areas are able remain on the surface for longer before reaching some threshold level of thermal or desiccation stress before retreating into the burrow to cool down and rehydrate. Increased surface time would confer a fitness advantage on male fiddler crabs because they can sustain longer periods of feeding activity (both inside and outside of the breeding period) and search for and court females for longer periods during the breeding period and so increase mating opportunities.

Once males retreated into the burrow, we observed was no difference in time spent in the burrow between habitats. This suggests that males are remaining on the surface until they hit some threshold of thermal/desiccation stress, then retreat into the burrow to cool down and rehydrate. Burrow temperatures do not differ between the two habitats (Munguia et al., 2017); thus recovery and rehydration take the same amount of time in both habitats.

Given that *A. mjoebergi* males show a strong preference for the mangrove habitat, one might expect these areas to be dominated by larger males, that are more successful at territory acquisition and defence (Jennions and Backwell, 1996; Morrell et al., 2005). However, we observed no difference in burrow diameter (as a proxy for crab size) between the two habitats. This may be due to the physical constraints of the habitat, with larger males being less adept at moving through the dense mangrove pneumatophores in some areas. A more likely explanation however, is that larger males are better able to tolerate the high surface and ambient temperatures of the open mudflat due to their higher thermal inertia and lower surface area:volume ratio (Allen et al., 2012). Smaller crabs may show a stronger preference for the mangrove habitat than large crabs because they are less likely to be able to tolerate the harsh conditions of the open mudflat. Although not directly tested here, such differences in preference, combined with the physical constraints of the mangrove pneumatophores may result in an even size distribution between the two habitats.

In conclusion, male fiddler crabs live and breed in a harsh environment with high surface and ambient temperatures and so are subject to thermal and desiccation stress. Although their burrow offers some respite from these harsh conditions, in order to feed, maintain condition and attract females, males must maximize their time above ground. In addition to using physiological mechanisms (e.g., blanching the carapace; Kronstadt et al., 2013; Munguia et al., 2013), and relying on their sexually-selected structures (Darnell and Munguia, 2011), male fiddler are able to mitigate the effects of these conditions to some extent, and therefore increase mating opportunities, by being selective about their choice of territory.

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Author contributions

MZD, PRYB, and PM conceived and designed the experiments. MZD, PRYB, JS, MLD, and PM performed the experiments. MZD, PRYB, and PM analyzed the data. MZD, PRYB, JS, MLD, and PM wrote the manuscript.

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